# INTERSPECIFIC HYBRIDIZATION BETWEEN NATIVE AND NATURALIZED CRATAEGUS (ROSACEAE) IN WESTERN OREGON

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Abstract

Morphological evidence for hybridization between *Crataegus douglasii* var. *suksdorfii* and *C. monogyna* in the southern Willamette Valley, Oregon, has been derived from a population with intermediate leaf morphology. Experimental hybridization resulted in an average fruit set of 42 percent in ♀ *C. douglasii* × ♂ *C. monogyna,* and 7 percent in ♀ *C. monogyna* × ♂ *C. douglasii* crosses. Hybrid pollen was 66 percent stainable with aniline blue-lactophenol compared with 95 percent for *C. douglasii* and 96 percent for *C. monogyna.* This is the first documented hybridization between a European and a northwestern North American species.

Hawthorns (*Crataegus,* Rosaceae) are known to hybridize where species are sympatric (Standish, 1916; Bradshaw, 1954; Robertson, 1974; Byatt, 1975, 1976). None of the documented cases of hawthorn hybridization, however, has involved a species native to North America and a European species. In western Oregon, the native hawthorn, *Crataegus douglasii* Lindl. var. *suksdorfii* Sarg., and an introduced European species, *Crataegus monogyna* Jacq., have come together within the last 100 years. The native species has black fruit, five styles, and mostly unlobed leaves; the introduced species has red fruit, a single style, and deeply lobed or laciniate leaves. Hybridization has produced a population of intermediate plants with black fruits, variable style number, and a wide range of leaf shapes. The evidence presented here for the hybrid origin of these intermediate individuals is based on leaf morphology, the results of crossing experiments, and pollen stainability tests. All information gathered thus far supports the hybridization hypothesis.

The study was conducted on the Cogswell-Foster Reserve, a 36-ha tract 40 km north of Eugene in Linn County, Oregon. The Reserve was acquired by the Nature Conservancy in 1969. *Crataegus douglasii,* the black hawthorn, is native to the Reserve and is found throughout the Pacific Northwest, especially along streams, ditches, and valley bottoms. English hawthorn, *C. monogyna,* was introduced onto the Reserve about 100 years ago (Lucile Foster, pers. comm., 1976). It has spread vigorously throughout the area, forming dense thickets under canopies of *Quercus garryana* Dougl. Intermediate individuals can be found throughout the Reserve but are especially common along fence lines in open areas, where many individuals are large annd produce abundant flowers and fruit. Increment cores suggest that most of these trees are less than 20 years old.

In May, both species and their putative hybrid bloom simultaneously, *C. monogyna* having the most abundant flowers. Hymenopterans and

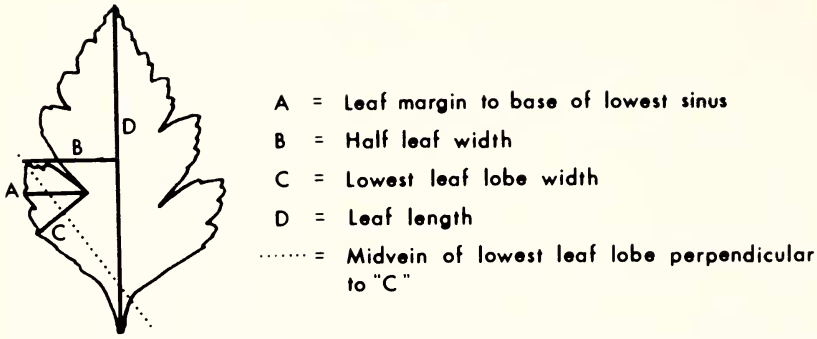


Fig. 1. Leaf measurements used in the scattergram (Fig. 2).

dipterans are attracted in large numbers. Honey bees (*Apis mellifera* L.) move among all three types on a single collecting flight. Frugivorous birds are known to be the principal agents of hawthorn seed dispersal (Hitchcock et al., 1969; Robertson, 1974) and are commonly seen devouring hawthorn fruits on the Reserve.

## Materials and Methods

*Leaf Variability.* Ten to 15 leaves from 114 randomly selected plants were collected in May and October, 1977. Four measurements were made on each leaf (Fig. 1).

*Artificial Crosses.* Hand crosses were made on May 1–13, 1976, and May 11–19, 1977. Crossing was done on calm, clear days, during midmornings and early afternoons. A corymb of 1–16 flowers was considered the "crossing unit" for each hybridization. Eighteen *C. douglasii* × *C. monogyna* crosses were made involving 203 flowers on 18 different plants. The pistillate parent was *C. douglasii* for ten corymbs and *C. monogyna* for eight corymbs. Hawthorn stigmas become receptive about two days before the petals open. Pollen is shed at anthesis. Therefore, flowers of the pistillate parent were chosen in the "popcorn" stage, just before bud opening. Stamens were removed with fine forceps, and pollen was transferred directly from the flowers of the male parent to the stigmas of the emasculated flowers. Corymbs were then bagged with cheesecloth and tied with string. Bags were opened in July to check fruit set and then reclosed to allow fruit ripening. All of the resulting fruits were saved for testing of seed viability.

Nine corymbs were bagged before bud opening to test for the necessity of pollen vectors. On eight plants, self-crosses were made to test for self-incompatibility, which has been reported in some Rosaceae (East, 1940).

*Pollen Viability Tests.* Pollen from 22 pressed hawthorn specimens was examined using aniline blue-lactophenol as an indicator (see Byatt, 1977). Percentages were based on microscopic examination of an aver-

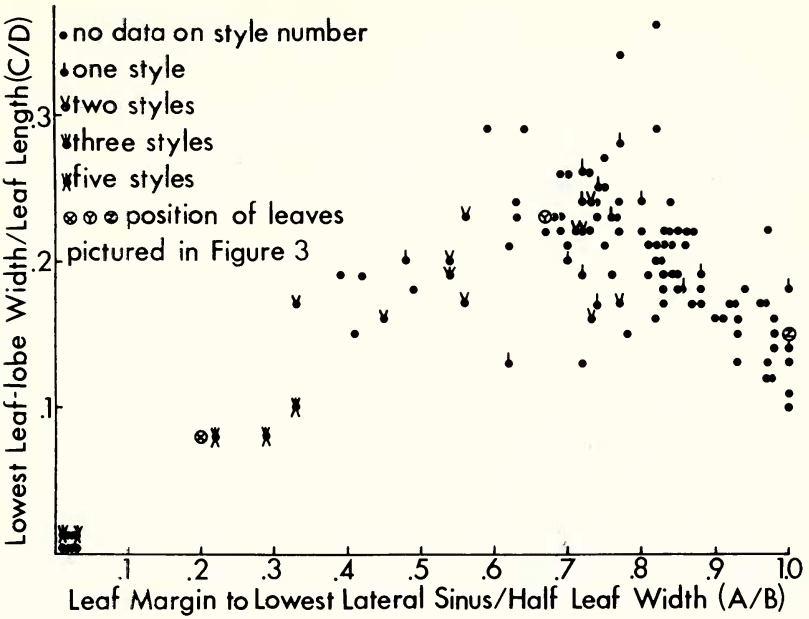


FIG. 2. Scattergram illustrating range of hawthorn leaf variability at the Cogswell-Foster Reserve. Each point represents the mean of leaves measured from an individual plant. One leaf each of *C. douglasii* (X), *C. monogyna* (Z), and an intermediate type (Y) from Fig. 3 are plotted to help indicate the relationship of leaf morphology to position on the scattergram.

age of 250 grains per plant. Grains that stained dark blue were assumed to be viable and unstained grains to be inviable.

## RESULTS

*Leaf Variability.* Mean relative distance from the leaf margin to the base of the lowest sinus (A/B) was plotted against the mean ratio of the lowest leaf lobe width to leaf length (C/D) for each plant (Fig. 2). Distribution of points on the scattergram suggests the presence of a "swarm" of hybrid types that overlap the parental types in leaf morphology. *Crataegus douglasii* leaves are unlobed or shallowly lobed; *C. monogyna* leaves are usually deeply lobed or laciniate; while leaves of intermediate plants show wide morphological variation (Fig. 3).

*Artificial Crosses.* There is cross compatibility between *C. douglasii* and *C. monogyna* as judged by the high percentage of fruit set in ♀ *C. douglasii* × ♂ *C. monogyna* crosses. Fruit formation on ten corymbs ranged from 25 to 73 percent of treated flowers, with mean fruit set at 42 percent. The mean fruit set for *C. douglasii* corymbs left open for insect pollination was 29 percent.

Fruit set was much reduced in ♀ *C. monogyna* × ♂ *C. douglasii* crosses. Five out of eight corymbs set no fruit. The highest fruit set on

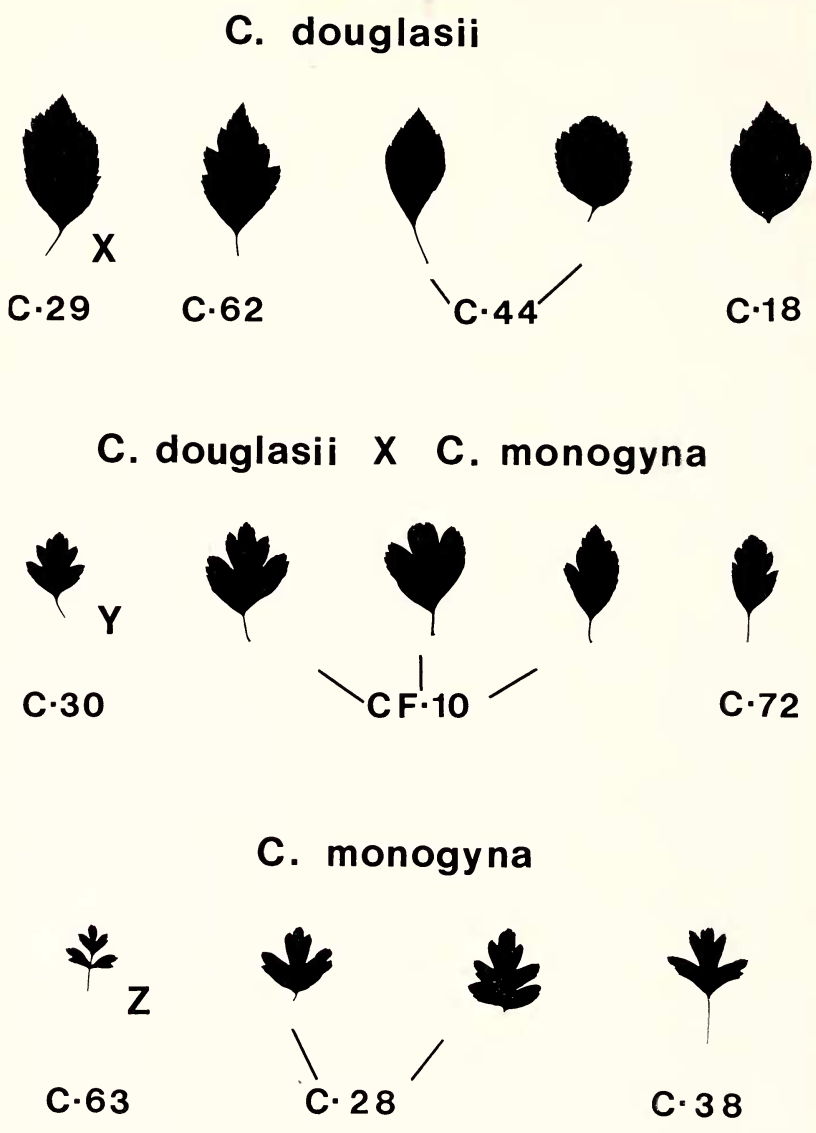


Fig. 3. Representative hawthorn leaf types from the Willamette Valley, Oregon. Letters and numbers refer to individual plants. Leaves X, Y, and Z have been plotted on the scattergram (Fig. 2).

one corymb was 25 percent and mean fruit set was 7 percent. Mean fruit set for *C. monogyna* corymbs left open to insects was 50 percent. The low fruit set is not thought to be an artifact of the experimental handling of *C. monogyna* flowers, because in other crosses, *C. monogyna* set significant amounts of fruit.

There was no fruit set on any corymb bagged before bud opening nor on any selfed corymb.

*Pollen Viability Tests.* Pollen from presumed hybrids showed significantly lower percentages of stainable grains than parental pollen. For pollen from nine individuals with hybrid morphology, the percentage of stainable grains ranged from 42 to 75 percent (mean = 66 percent). Stainable pollen from five specimens of *C. douglasii* ranged from 93 to 98 percent (mean = 95 percent); and from eight specimens of *C. monogyna,* stainability ranged from 93 to 98 percent (mean = 96 percent).

At least one hybrid individual at the Cogswell-Foster Reserve is completely male-sterile, all flowers having vestigial stamens that lack anthers. This plant is vegetatively vigorous, flowers heavily, and sets some fruit.

A comparison of the Willamette Valley hawthorns is given as Table 1.

## Discussion and Conclusions

Evidence that the native *Crataegus douglasii* var. *suksdorfii* hybridizes with the introduced *Crataegus monogyna* in western Oregon can be summarized as follows:

1. There are many plants intermediate in leaf shape and style number and possessing a novel combination of parental characters: distinctly lobed leaves and black fruits.

2. Interspecific crosses resulted in substantial fruit set when *C. douglassii* was the pistillate parent. Partial unilateral sterility appears to be occurring because reciprocal crosses resulted in reduced fruit set. Insect vectors appear necessary for pollination, and all plants tested exhibited self-sterility.

3. Pollen stainability tests indicated significantly lower percentages of viable pollen grains in the putative hybrids than in the parents.

Most of the *C. douglasii* × *C. monogyna* hybrids on the Cogswell-Foster Reserve have 3–5 lobed leaves and 2–3 styles and, when in bloom, match the key description of *Crataegus oxyacantha* L., another hawthorn of European origin that is naturalized in the Pacific Northwest. [*C. oxyacantha* is now known in Europe as *C. laevigata* (Poiret) DC. See Byatt, 1974.] Hawthorn samples from the Reserve were sent to J. Byatt, Westfield College, London, whose determinations support the hybrid nature of the intermediate plants and confirm that they are not *C. oxyacantha*. Dr. Byatt reports (pers. comm., 1977) that *C. oxyacantha* is never black-fruited. She also writes, "It has already been sug-

TABLE 1. SOME DIAGNOSTIC CHARACTERS OF *Crataegus douglasii* VAR. *suksdorfii*, *C. monogyna*, AND THEIR HYBRIDS FROM THE WILLAMETTE VALLEY, OREGON.

| Character | *C. douglasii* | Hybrids | *C. monogyna* |
|---|---|---|---|
| Petal color | White | White | White or pink |
| Style and pyrene number | 5 | (1) 2–3 (4) | 1 |
| Receptacle | Glabrous | Glabrous to hairy | Mostly hairy to woolly |
| Mature fruit color | Black | Black (Imm.: purple or red) | Red |
| Fruit shape | Globose | Globose | Ovoid |
| Mature leaf shape | Elliptic | Elliptic to obovate | Ovate or obovate |
| Leaf lobing | Unlobed or shallowly lobed | Variously lobed; sinuses of intermediate depth | Deeply lobed or laciniate |
| Leaf length | 2–9 cm | 1.5–6 cm | 1.5–3.5 cm |
| Leaf pubescence | Both surfaces pubescent to glabrate | Glabrous to somewhat hairy, or with some hairs on veins below | Glabrous except for patches of hairs in axils of veins beneath |
| Leaf margins | Serrate or biserrate | Serrate or toothed | Entire or sparingly serrate |
| Lowest lateral leaf veins | Straight | Straight or slightly recurved | Strongly recurved |
| Termination of lateral veins | At tooth apices | Variable | At apices and sinuses |
| Fruit ripens | Jul–Aug | Aug–Sep | Sep–Oct |
| Chromosome number | $2n = 34$ (Calder et al., 1968) | ——— | $2n = 34$ (Clapham et al., 1962) |
| Geographic range | B. C. to S OR, W of Cascades | Willamette Valley, OR; possibly elsewhere | Eurasian native; naturalized sparingly but widely in N. A. |

gested that black fruit colour is dominant in crosses between red and black-fruited taxa." This agrees with our observation that all presumed hybrids on the Cogswell-Foster Reserve are black-fruited.

Hitchcock et al. (1969) list both *C. monogyna* and *C. oxyacantha* as naturalized elements of our flora, distinguishing between them on the basis of leaf lobing and style number. Both are described as red-fruited. *Crataegus douglasii* × *C. monogyna* hybrids and *C. oxyacantha* may be distinguished in future treatments on the basis of fruit color.

*Crataegus monogyna* may be hybridizing with another North American species. J. B. Phipps (pers. comm., 1977) has noted probable hybridization between *C. monogyna* and the native *C. punctata* Jacq., in Ontario, Canada.

In this study we describe what we believe to be the first documented case of hybridization between a western North American species and a European native. At the present time, *C. douglasii* × *C. monogyna* hybrids are known only from Linn County in the Willamette Valley; however, they can be expected to occur in other locations in western British Columbia, Washington, and Oregon, where the parent species have coexisted for some time.

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